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Neural entrainment to visual rules in infant and adult brain

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Visual Rule Learning (RL) is a key cognitive ability allowing the detection and generalization of repetition-based rules in a continuous stream. Most studies on visual RL focus on post-exposure behavioral tasks, missing the learning process dynamics and the individual and age-related differences. Here, for the first time, we used neural entrainment to investigate visual RL, particularly in infants. Thirty adults and 27 nine-month-old infants were exposed to triplets of shapes in an ABA structure for 2 min while recording EEG. Triplets appeared at 6 Hz, with the embedded rule frequency at 2 Hz. Behavioral tests assessed rule discrimination between familiar (ABA) and novel patterns, measuring infants' looking behavior and adults' familiarity judgments. Results revealed a striking infant advantage: infants exhibited greater neural sensitivity to the rule frequency and a faster learning trajectory than adults. Adults showed stronger neural entrainment at the base frequency, particularly in frontal regions, reflecting developmental shifts in endogenous attention and salience processing. Importantly, in infants, neural response increased with repeated ABA exposure, correlating with successful rule discrimination, whereas adults showed no such progression. These findings provide the first evidence of an infant advantage in abstracting patterns from sensory input, supporting a general RL mechanism.

Keywords Visual rule learning, Infants, Adults, Neural entrainment

Sensory input in our environment is far from random. It is characterized by a significant amount of hidden structure and spatiotemporal regularities within a continuous flow of complex and multi-timescale information. To be effectively processed and interpreted by the brain, this sensory input must be separated from noise, parsed and grouped into meaningful segments[1]. Successful rapid extraction of spatiotemporal pattern information from the environment underpins many complex behaviors, including recognizing meaningful actions in social interactions, and the intricate process of language acquisition (e.g.,[2]). These are just a few examples of the critical role of structure processing in successful adaptation to the environment.

Sequences of images, sound, and linguistic information can be stored at various levels of detail, ranging from specific items and their timing to abstract structures. Dehaene et al.[3] identified five distinct systems capable of representing sequence knowledge with increasing levels of abstraction: (1) transition probabilities and timing, associated with statistical learning (SL); (2) chunking; (3) ordinal knowledge; (4) rule-based patterns, linked to rule learning (RL); and (5) nested hierarchical structures, such as tree representations. While prior electrophysiological work with infants has primarily focused on infants' ability to learn patterns defined by the statistical properties of sequences (the first three levels in Dehaene's taxonomy), the present study investigates the more abstract and complex mechanism of RL.

RL involves the identification of repetition-based patterns—such as adjacent-repetition rules (e.g., ABB, AAB) or non-adjacent repetition rules (e.g., ABA)—from perceptual input, and their generalization to novel items that share no surface features[4]. Crucially, RL allows learners to extract high-order regularities that are independent of the specific perceptual features of individual items, enabling generalization beyond the surface characteristics of the stimuli. Therefore, this mechanism is foundational to discovering and generalizing increasingly complex and abstract structures, including those involved in grammar learning (e.g.,[5–7]). Extensive evidence suggests that RL is a widespread and fundamental cognitive mechanism observed across species (e.g., primates and rodents;[8]), perceptual domains (e.g., visual and auditory,[4,9]), and developmental stages (especially from birth to childhood, e.g.,[10]).

During development, RL undergoes significant changes. In the auditory domain, newborns can detect repetition-based patterns, particularly those involving adjacent repetitions (e.g., ABB), but show limited

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sensitivity to non-adjacent repetitions (e.g., ABA;[11]). By 4 months, this ability extends to ABA patterns in musical chords and tones. However, by 7 months, the capacity to learn these patterns appears to tune to the stimuli to which infants are more exposed (e.g., speech)[12], suggesting a potential experience-driven decline in the spectrum of RL capacities during development. RL skills also exhibit developmental trajectories in the visual domain. A crucial factor in modulating visual RL in infants is the spatiotemporal layout of the visual display. Indeed, by 3–4 months, infants can extract and generalize ABB and ABA patterns in static spatial displays[13], and by 8 months they can process these patterns sequentially in left-to-right arrangements[9]. However, when spatial information is lacking and only temporal information is provided, resembling the auditory domain (i.e., central, transient pattern presentation), younger infants fail to extract visual non-adjacent repetition ABA patterns, while older infants from the age of 11 months succeed[14], just like older children[15] and adolescents[16]. Despite evidence suggesting developmental changes in RL capabilities, direct comparisons of learning strength across infants, older children, and adults are lacking, leaving the exact developmental trajectory of RL under debate.

RL abilities in infants have primarily been demonstrated using post-exposure behavioral tasks. These tasks have extensively documented novelty responses after learning, revealing what has been learned but offering limited insight into the underlying learning processes themselves, particularly in the visual modality (e.g.,[17]). Recent findings have begun to characterize the neural signature of pattern learning in the auditory domain, moving beyond the post-exposure measures. For example, neuroimaging studies using NIRS have shown that the newborn brain is sensitive to rule-based adjacent repetitions in speech sequences (e.g., ABB;[11]). Indeed, newborns exhibited a greater neural response to ABB compared to random ABC patterns from the very onset of exposure, and this initial advantage for ABB patterns increased in temporal and frontal regions over time. In contrast, newborns did not discriminate between structures comprising more complex non-adjacent ABA repetitions and ABC patterns, aligning with behavioral studies that suggest non-adjacent repetitions pose greater challenges for the newborn brain. These findings suggest the presence of an automatic perceptual mechanism for detecting repetitions. Moreover, the increased frontal brain activity observed during ABB processing may be associated with later stages of learning or memory processes, such as the consolidation of high-order structure representations (e.g.,[18,19]).

Surprisingly, the underlying neural mechanisms of infants' RL in the visual domain remain relatively unexplored. This learning process emerges from an interplay between domain-general and modality-specific mechanisms (see 1). For instance, vision—specialized for processing spatial information—facilitates rule extraction through spatiotemporal layout (e.g.,[13]), while audition—optimized for temporal analysis—supports rule extraction through temporal patterns (e.g.,[1]). These modality-specific biases influence how stimuli are perceived, maintained in short-term memory, and integrated into a coherent representation (e.g.,[20–22]).

Recent electrophysiological studies have applied the frequency tagging (FT) method to investigate infants' ability to extract transitional probabilities (i.e., statistical learning) embedded in speech (e.g.,[23]) and visual[20] streams. FT allows researchers to identify neural responses to specific stimuli by presenting them periodically at a given frequency and measuring sharp peaks in the EEG power spectrum at the corresponding frequency[24]. Evidence in adults shows that FT reveals robust entrainment for rhythmic and quasi-rhythmic or variable presentation sequences[25], highlighting that multiple cortical areas are sensitive to temporal structure and can flexibly track dynamic visual stimuli. FT can also capture attentional modulation and selective processing in specialized cortical areas, reflecting its sensitivity to both stimulus-driven and top-down influences[26,27]. Moreover, this technique is particularly valuable to directly compare neural responses between adults and infants. In the auditory domain, Choi et al.[23] reported that infants, like adults, initially synchronize neural activity to syllables at the onset of exposure to a speech sequence. As exposure continues, neural responses progressively entrain to the frequency of recurring statistical patterns, facilitating the grouping of syllables into words. Over the course of learning, the neural 'word learning index' increases logarithmically, likely reflecting infants' growing ability to detect word boundaries from isolated syllables within the continuous stream of speech. Importantly, this neural sensitivity to word boundaries is positively correlated with infants' ability to discriminate between familiar words (presented during the exposure phase) and novel words (composed of the same syllables but in a new order). In the visual domain, however, Capparini et al.[20] showed that 4- to 6-month-old infants exhibit neural entrainment to both individual shapes and pairs of shapes organized as doublets based on deterministic transitions. While sensitivity to these doublets emerges early during the exposure period, no discernible learning curve is observed. Also, adults were not included in this study. These findings suggest a potential key difference between auditory and visual SL: In the auditory domain, statistical learning may follow a gradual trajectory, which likely reflects infants' increasing ability to detect statistical regularities in the input. In contrast, visual statistical learning may result from rapid initial sensitivity to simple visual patterns followed by a plateau in learning.

While these studies have successfully applied the FT method to investigate sensitivity to statistical patterns and have directly compared the neural response in infants and adults, the present study aims to examine the neural processes underlying the extraction of rule-like structures—ABA—embedded within sequences of visual items. Differently from previous studies investigating infants' neural entrainment to statistical patterns, which focused on pattern recognition (where test items match habituation items), the present study examines generalization, which requires an abstract representation of the pattern in which items can be replaced. Given that visual RL is fully operative starting from 8 to 11 months, with infants able to detect non-adjacent repetitions—an indicator of more complex structures (e.g.,[14])—even when stimuli are presented centrally, we opted to test 9-month-old infants and adults. We used FT to collect neural data during the initial exposure phase to explore the dynamics of learning as it unfolds; this approach is well-suited to accommodate the brief duration of focused attention typically observed in infants[23]. The study's goals were threefold: (1) to characterize the neural responses underlying visual RL skills in both infants and adults, investigating potential differences between these age groups; (2) to examine the learning curve during exposure to the rule-based sequences, as reflected in neural entrainment over time; and (3) to investigate the relationship between the strength of neural entrainment and learning outcomes, specifically the ability to both identify and generalize the learned rule to novel sequences.

Using high-density EEG, participants were exposed to a continuous 2 min stream of shapes organized into ABA structures. Each shape was presented at a frequency of 6 Hz, while the frequency of triplets was 2 Hz. We examined neural responses at these two frequencies to track distinct processing steps: the 6 Hz response served as a baseline, confirming reliable processing of the individual visual stimuli, whereas the 2 Hz response specifically indexed the neural processing of the triplet structure. Crucially, we also examined how neural responses at both frequencies dynamically evolved over the course of exposure by time-locking the data to twelve consecutive 10 s epochs spanning the 120 s exposure duration. This allowed us to explore learning-specific changes in entrainment at the rule frequency (2 Hz) as well as changes in general visual response (6 Hz) across the exposure period. Immediately following the learning phase, adults and infants were presented with six familiar (ABA) and six novel (ABB) test sequences instantiated by a new set of shapes to assess their ability to generalize the learned rule to novel items. Infants' rule generalization was assessed behaviorally by recording differential looking times to the novel versus familiar sequences, whereas adults' generalization was measured by their accuracy in explicitly recognizing the familiar and novel rules. We first predicted that both infants and adults would exhibit neural entrainment to both individual shapes (6 Hz) and the ABA patterns (2 Hz). Second, we hypothesized that the strength of entrainment to the ABA rule during the familiarization phase would correlate with subsequent behavioral performance: specifically, with the magnitude of infants' preference for the novel rule (ABB) and with adults' discrimination accuracy between familiar and novel rules during the test phase. This finding would align with previous findings in adults[28] and infants[23], showing a link between neural entrainment and behavioral learning outcomes[23]. We focused our analyses on occipital and frontal brain regions, consistent with previous research on pattern learning with auditory stimuli in infants (e.g.,[11]) and adults[29].

Results

Learning phase

To examine neural entrainment during the learning phase, we first visualized and summarized the spectral data. The baseline-corrected amplitudes (BCA) of the grand-average spectrum obtained via Fast Fourier Transform (FFT) and the signal-to-noise ratio (SNR) are graphically represented in Figs. 1 and 2, respectively. For means and standard deviations of the mean z-score and SNR values for the rule (2 Hz) and base (6 Hz) frequency responses, see SI Appendix, Table S1. We conducted separate analyses for the rule frequency (2 Hz) and the base frequency (6 Hz) to assess whether each elicited a distinct neural response, reflecting the processing of individual shapes versus the triplet structure.

To investigate age group differences in neural response at the rule frequency (2 Hz), we ran two separate linear mixed-effect models (LMMs) on BCA amplitudes at the occipital and frontal Regions Of Interest (ROIs). For the occipital area, the model revealed significant main effects of Group, $F(1,55) = 50.878$, $p < 0.001$, indicating higher BCA in infants compared to adults, and ROI, $F(2,680) = 21.195$, $p < 0.001$, indicating a stronger response in the medial ROI compared to the lateral ones ($ps < 0.001$). The Group x ROI interaction was also significant, $F(2,680) = 17.184$, $p < 0.001$, confirming that BCA amplitudes were larger in infants than in adults across all three occipital ROIs (left, middle, and right) ($ps < 0.001$), and that they were significantly larger across the medial ROI compared to the lateral ones ($p < 0.001$) only in infants. The LMM conducted on the frontal ROIs revealed a significant Group main effect, $F(1,55) = 9.104$, $p = 0.004$, due to BCA amplitude being larger in infants ($M = 0.3557$, $SE = 0.063$) than in adults ($M = 0.0925$, $SE = 0.060$). No other effect was significant ($ps > 0.3$) (Fig. 2a).

Consistent with the rule frequency analysis, base frequency (6 Hz) BCA amplitudes were also analyzed separately for the occipital and frontal ROIs. For the occipital area, the model revealed significant main effects of Group, $F(1,55) = 12.819$, $p < 0.001$, and ROI, $F(2,680) = 36.16$, $p < 0.001$. The signal was significantly stronger in the infant ($M = 1.238$, $SE = 0.133$) compared to the adult ($M = 0.579$, $SE = 0.127$) group, and in the medial ROI ($M = 1.185$, $SE = 0.097$) compared to both the right ($M = 0.863$, $SE = 0.0994$, $p < 0.001$) and the left ($M = 0.677$, $SE = 0.099$, $p < 0.001$) ROIs. The signal in the right ROI was also overall stronger than in the left ROI ($p < 0.0001$). The interaction between Group and ROI was also significant, $F(2,680) = 36.2$, $p < 0.001$, revealing that the age group difference in BCA values (infant BCA larger than adult BCA) was confined to the medial ROI ($p < 0.001$), and the amplitude differences across ROIs were significant for the infant group only (medial larger than right and left, $ps < 0.017$). The model conducted on BCA amplitudes for the frontal area revealed a main significant effect of group, $F(1,55) = 7.0162$, $p = 0.01$, due to amplitudes being larger in the adult ($M = 0.302$, $SE = 0.0410$) than in the infant ($M = 0.144$, $SE = 0.043$) group. No other effects reached statistical significance ($ps > 0.8$) (Fig. 2b).

Temporal dynamics of neural entrainment

To examine learning-related changes in neural entrainment at the rule frequency (2 Hz) and changes in the general visual responses at the base frequency (6 Hz) across the exposure period, BCA amplitudes were analyzed, separately for each frequency, across the twelve 10 s epochs of the 120 s exposure period using separate LMMs for each age group and scalp ROIs. At the rule frequency of 2 Hz, infants' frontal activity remained stable across the 10 s epochs ($p > 0.15$). In contrast, occipital response showed a linear decrease over the course of learning, $F(2,26) = 18.1714$, $p < 0.001$, with a steeper slope in the medial ROI compared to both the left and right ROIs ($ps < 0.001$), as evidenced by a significant ROI x Segment interaction, $F(4,4151) = 9.832$, $p < 0.001$. Unlike infants, adults showed stable activity at the rule frequency in both occipital and frontal ROIs across triplet exposures ($ps > 0.48$) (Fig. 3).

Analyses of the base frequency BCA amplitudes revealed distinct temporal dynamics of neural response across the epochs in the frontal and occipital ROIs for both age groups. In infants, frontal activity showed a significant linear increase, $F(2,25.99) = 4.7516$, $p < 0.017$, while occipital responses displayed an inverted linear and quadratic decrease, $F(2,26.1) = 14.816$, $p < 0.001$, with a steeper slope in the medial ROI compared to the

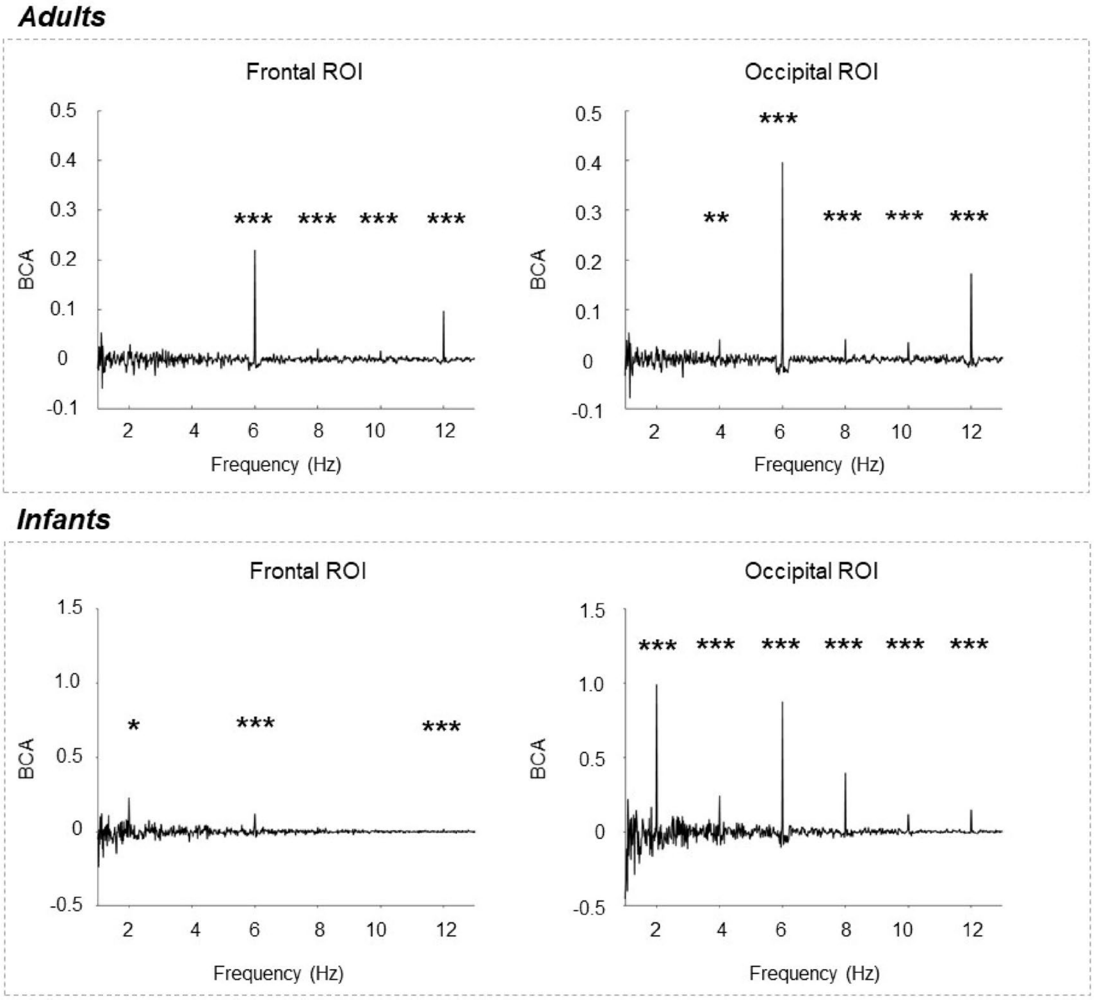


Fig. 1. Baseline-corrected amplitude (BCA) for adults (top) and infants (bottom), shown separately for the frontal and occipital ROIs. Please note that the y-axis varies between age-groups due to stronger responses in infants. Occipital ROI: * $Z > 2.65$; ** $Z > 3.09$; *** $Z > 3.72$. Frontal ROI: * $Z > 2.75$; ** $Z > 3.34$; *** $Z > 3.77$.

left and right ROIs (*ps* < 0.001; ROI x Segment, $F(2,4151) = 13.928$, $p < 0.001$). In the adult group, activity in the frontal ROI showed a marginal quadratic increase with increasing exposure, $F(2,28.998) = 3.121$, $p = 0.059$, while occipital activity remained stable throughout exposure ($p > 0.13$) (Fig. 3).

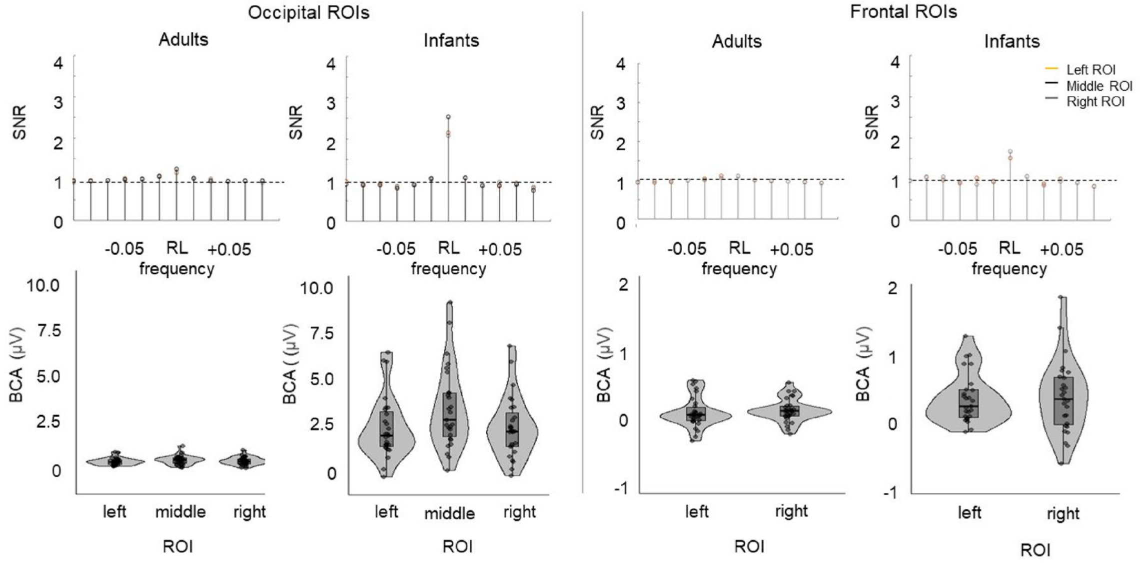
Test phase

To assess behavioral learning outcomes during the test phase, rule generalization ability was quantified using rule recognition accuracy in adults and differential looking times to the familiar (ABA) versus novel (ABB) sequences in infants. For the adult group, a one-sample *t*-test revealed significantly above-chance performance in discriminating the familiar from the novel rule, $t(27) = 3.014$, $p = 0.006$, Cohen's $d = 0.570$, with an average accuracy of 0.601 ($SE = 0.034$). For the infants' group, the LMM analysis revealed a significant effect of test trial pair ($B = -0.30314$, $SE = 0.091$ $t = 3.334$, $p < 0.002$, indicating a decrease in overall looking time across the test phase. Post hoc Bonferroni-corrected tests showed that infants looked significantly longer at the first test trial pair ($M = 1.134$, $SE = 0.059$) compared to the third pair ($M = 0.929$, $SE = 0.0594$, $p < 0.001$ Bonferroni corrected). Crucially, a significant Test Trial Pair x Test Trial Type interaction was observed ($B = -0.308$, $SE = 0.129$, $t = -2.392$, $p = 0.018$). Post hoc analyses revealed that this interaction was driven by significantly longer looking times to novel stimuli ($M = 1.012$, $SE = 0.068$) compared to familiar stimuli ($M = 0.841$, $SE = 0.068$, $p = 0.009$) within the third trial pair only.

Relation between learning and test

To investigate whether neural responses during learning predicted behavioral outcomes, we examined the relationship between rule-frequency (2 Hz) BCA amplitudes and participants' performance at test. Multiple regression analyses revealed a significant association between rule frequency (2 Hz) BCA amplitudes in the occipital ROI during the first and second halves of the learning phase and infants' log-transformed novelty preference scores, $F(2,20) = 12.02$, $p < 0.001$, explaining 55% of the variance. Notably, these associations

a) 2 Hz frequency



b) 6 Hz frequency

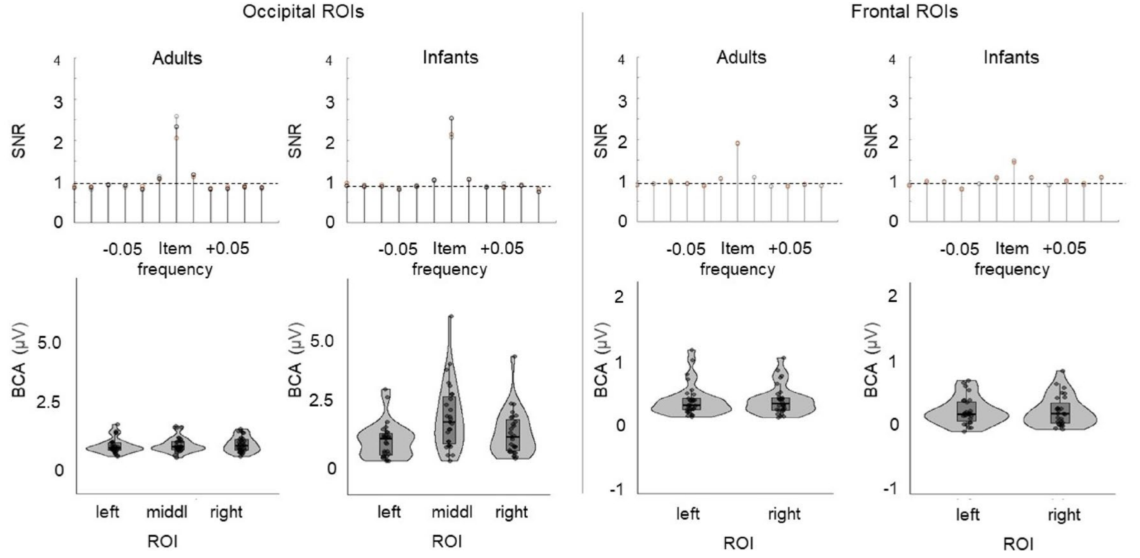


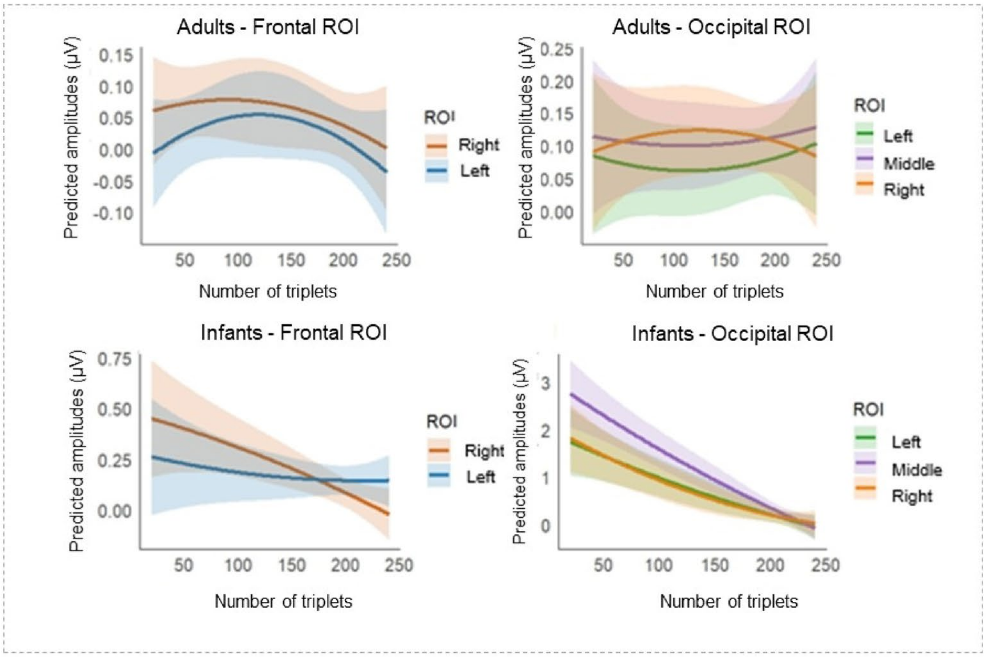
Fig. 2. (**a**) Top: Signal-to-Noise Ratios (SNRs) for adult and infant samples at the rule frequency. Bottom: Baseline-Corrected Amplitude (BCA) for adult and infant samples at the rule frequency, computed for occipital and frontal ROIs. Individual data points represent subject-level means. (**b**) Top: Signal-to-Noise Ratios (SNRs) for adult and infant samples at the item frequency. Bottom: Baseline-Corrected Amplitude (BCA) for adult and infant samples at the item frequency, measured in the occipital and frontal ROI.

differed between learning epochs and exhibited opposing directions. Specifically, occipital activity at the rule frequency during the first 60 s segment was positively associated with novelty preference scores ($B = 0.00976$, $SE = 0.00417$, $t(20) = 2.34$, $p = 0.03$), whereas neural response during the second 60-s segment was negatively associated ($B = -0.02167$, $SE = 0.00439$, $t(20) = 4.94$, $p < 0.001$) (Fig. 4). This pattern suggests that infants with stronger occipital responses at the rule frequency during the earlier stages of learning showed higher novelty preference, while those whose occipital activity was stronger at the end of learning showed reduced novelty preference or even a shift toward familiarity preference. Unlike in the occipital ROI, analysis of the frontal ROI did not reveal any significant association with novelty preference scores ($p > 0.189$). For the adult group, no significant relationship was observed between the rule BCA amplitude in either the occipital or frontal ROI and the proportional accuracy during the test phase (ps > 0.223).

Discussion

This study is the first to explore the neural correlates of visual RL in infants and adults during stimulus exposure, using EEG frequency-tagging to track neural entrainment to non-adjacent repetition-based ABA patterns

Rule frequency (2 Hz)



Base frequency (6 Hz)

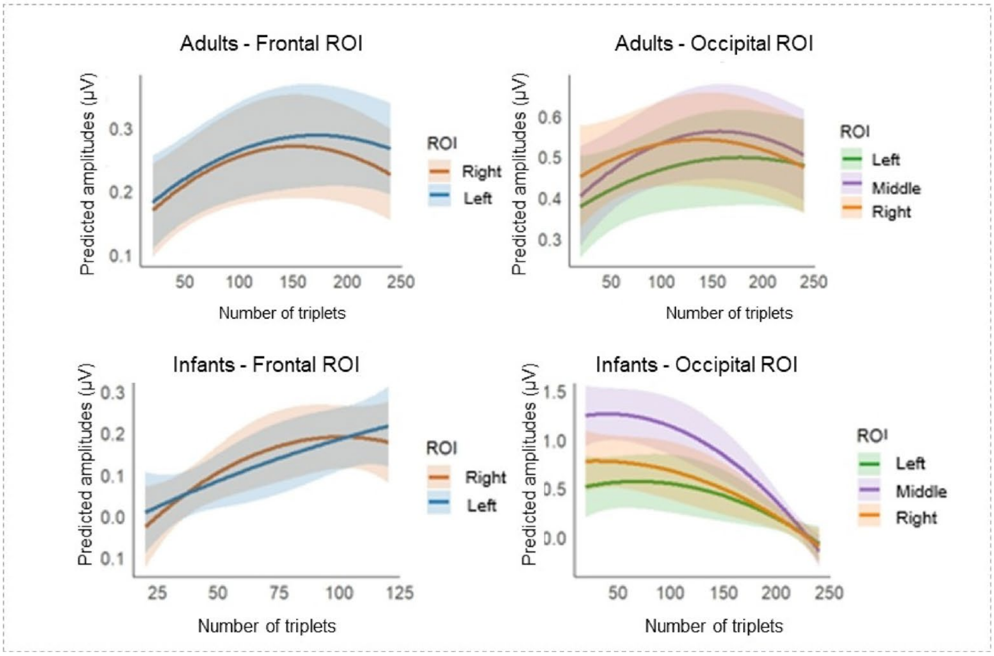


Fig. 3. Mean baseline-corrected amplitude (BCA) for the adult and infant samples at the rule frequency (2 Hz) (top) and the item base frequency (6 Hz) (bottom) measured at frontal and occipital ROIs. Lines indicate model-predicted amplitudes with 95% confidence intervals.

within a continuous visual stream. While frequency-tagging has been utilized to explore infants' statistical learning of transitional probabilities in the auditory (e.g.,[23]) and visual[20] domains, its application to rule learning mechanisms represents a significant advancement. Despite established behavioral evidence of visual RL in infants[9,10], the neural dynamics during stimulus exposure remain largely unknown. To bridge this gap, we examined and compared neural entrainment to the frequency of the individual shapes (base frequency, 6 Hz and harmonics) and the frequency of the repeating ABA patterns (rule frequency, 2 Hz and harmonics) in infants and adults, and analyzed its relationship to learning outcomes. Our results show that both infants' and adults'

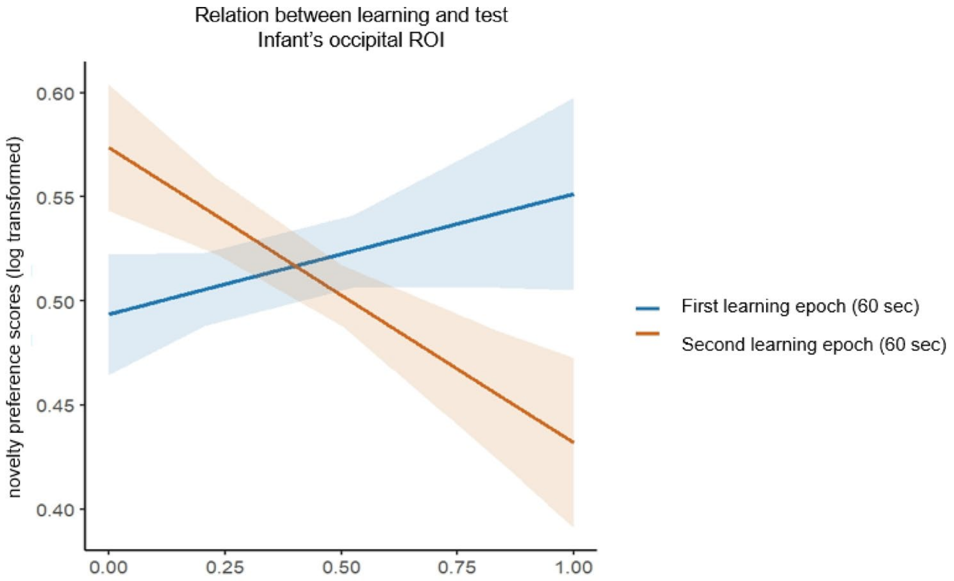


Fig. 4. Regression of infants' log-transformed novelty preference scores against rule frequency (2 Hz) BCA amplitudes in the occipital ROI showing a positive association during the first 60 s learning epoch and negative association during the second 60 s learning epoch. Lines show model-predicted values with 95% confidence intervals.

brain activity synchronized with the rule and base frequency across occipital and frontal regions. These findings are the first to reveal infants' and adults' efficient extraction and representation of rule-based patterns within rapid visual streams (6 Hz, ~ 167 ms presentation duration), consistent with auditory processing findings[23].

Despite exhibiting significant neural tracking of the ABA rule in both groups, our results suggest distinct neural processing strategies for rule learning in infants and adults. Infants' response was significantly stronger than that of adults in both occipital and frontal ROIs, with a particularly robust and widespread response in the occipital ROI, suggesting heightened sensitivity to repetition-based dependencies within the infant visual cortex. These findings align with previous evidence of efficient occipital entrainment to statistical regularities in streams of continuously presented visual stimuli in 4–6-month-old infants[20], consistent with the notion that the infant brain is particularly adept at extracting and representing visual structure, facilitating rapid learning and adaptation[1,30,31].

A group difference emerged also in the analysis of base frequency responses. While both groups exhibited significant tracking of the individual shapes in both occipital and frontal ROIs, occipital activity was stronger in infants while frontal activity was stronger in adults. Assuming that the base response is primarily driven by attentional processes[24,32,33], this finding may reflect a fundamental difference in task approach between the two age groups, with infants relying predominantly on bottom-up processing and exogenous attention, and adults recruiting top-down endogenous attention strategies. It remains an open question whether adults would dynamically adjust their attentional strategy or engage frontal areas more actively with prolonged exposure, potentially reflecting gradual shifts in top-down control in a free-viewing task as employed here. The observed marginal trend of increasing activity in the frontal ROI is consistent with this possibility. Future studies should examine measures sensitive to top-down processes, such as EEG alpha activity and pupil diameter, which have been shown to reflect endogenous attention switching and listening effort, respectively[34].

This idea that task approach reflects developmental changes in endogenous attentional processes possibility aligns with the observed differences in rule frequency (2 Hz) learning trajectories during exposure to the ABA triplets[1]. Specifically, infants exhibited a rapid and significant linear decrease in occipital entrainment to the triplets across the twelve 10 s epochs of the learning phase, whereas the adults' rule-frequency (2 Hz) response remained temporally stable in both occipital and frontal ROIs. Consistent with this interpretation, prior work shows that frontal regions can modulate visual processing and attentional weighting, selectively enhancing relevant input features and dynamically shaping cortical representations[26,27]. While stable occipital activity in adults may reflect efficient top-down control on sensory processing, the decreasing occipital activation in infants may be attributed to low-level learning-related processes such as neuronal adaptation (e.g.,[35,36]), resulting from rapid and automatic detection of positional repetition cues, potentially akin to the perceptual repetition detector proposed by Gervain et al.[11] for auditory processing in newborns. Given the immaturity of the frontal cortex, infants primarily rely on bottom-up processing, where cognitive resources are captured by salient features in the environment. Similar to how infants benefit from stimulus-driven attention to prosodic information to simplify the complex speech input in language acquisition[37] and to repetitions for grammar acquisition[38], stimulus-driven attention to positional repetition cues may facilitate rapid learning of rule-like patterns in the visual domain. Notably, studies in adults have shown that downregulation of prefrontal cortex control via transcranial magnetic stimulation fosters visual statistical learning of non-adjacent dependencies[39] and associative learning of grammatical dependencies in artificial language stimuli[40], further supporting the potential benefits of limited top-down control in early learning.

Overall, infants showed greater neural sensitivity and learning progression to the rule frequency (2 Hz) compared to adults. This finding, which emerged despite the infants' noisier data and greater behavioral interference, contrasts with previous FPVS studies that have typically reported stronger entrainment responses in adults (e.g.,[23,41]). This pattern highlights infants remarkable efficiency in extracting repetition-based structures within a rapidly presented stream of variable shapes. On the other hand, entrainment at the base frequency over the frontal ROIs was stronger in adults, suggesting a developmental shift potentially reflecting changes in stimulus salience mediated by attention. This shift is possibly related to the contrasting predictability of the recurring triplets and the individual shapes (e.g.,[42]). While the first image in each sequence consistently predicted the final image with 100% accuracy, establishing a strong, deterministic relationship between the first and the last shapes, each image was randomly drawn from a pool of 12, introducing high variability and low predictability of the shapes' features (form and color). Within the predictive coding framework[43], the brain generates top-down predictions about sensory inputs based on prior knowledge, that are constantly updated through incoming bottom-up information. When these predictions align closely with incoming stimuli, less cortical activity is required, resulting in minimal signal modulation. In this context, the smaller neural entrainment and the absence of a learning curve to the rule frequency in adults suggest that they processed information primarily at the shape-level, optimizing learning efficiency by focusing on unpredictability and filtering out predictable cues (rule patterns). In contrast, infants, relying more heavily on exogenous attention, were more readily captured by the salient non-adjacent repetitions within the shape stream, leading to enhanced neural response to the triplet frequency. While this interpretation offers a plausible explanation for the observed results, it remains speculative. Future studies should systematically manipulate the variability and predictability of stimuli to directly test this hypothesis, and further elucidate how developmental changes influence attentional priorities and learning mechanisms.

Time modulation effects in neural entrainment observed at the shape frequency align with this interpretation, suggesting developmental differences in the formation and updating of memory traces of the individual shapes' features[44–46]. Indeed, while variations in occipital activity in both groups mirrored those observed at the rule frequency, frontal activity increased progressively, with a linear pattern in infants and an inverted U-shaped pattern in adults. During the initial exposure period, repeated presentation led to enhanced neural processing, reflecting the formation and strengthening of internal representations. Subsequently, neural responses in adults decreased as their memory traces of shape identities stabilized. In contrast, 120 s of continuous exposure was not sufficient for infants to exhibit a similar pattern of decreasing activity, suggesting that they were still actively forming and refining their internal representations of the individual shapes throughout the exposure period.

The active and dynamic engagement of the infants' visual cortex in extracting and representing rule-based patterns is further supported in our data by the association between the strength of neural entrainment to the ABA triplets and learning outcomes. Infants who exhibited stronger neural entrainment to the ABA triplets during the initial exposure period (first 60 s) showed higher novelty preference during the test phase, as measured by longer looking times to the novel than the familiar rule. Conversely, infants whose neural response to the ABA rule was stronger during the final part of the exposure period showed less evidence of recognizing the familiar rule. This pattern of results implies that the temporal dynamics of occipital activation to the rule frequency are predictive of infants' ability to generalize the learned rule to novel stimuli and contexts. Specifically, early robust entrainment to the ABA rule appears to be crucial for successful rule learning and generalization, further pointing to the rapid and automatic nature of infants' detection of positional repetition cues in favoring successful pattern learning.

It is noteworthy that both infants and adults successfully discriminated between the familiar and the novel rule during the test phase, despite significant changes in the perceptual context (i.e. new shapes). Adults successfully extracted the underlying rules, achieving an average accuracy of ~ 60%, which is consistent with performance typically observed under incidental learning conditions (e.g., 26). Consistent with previous behavioral research on infant RL, successful learning in the current study was inferred from infants' generalization of the learned rule to novel items with altered surface features (form and color). However, the current study introduced an additional layer of novelty by presenting the test stimuli at a much slower pace than during the learning phase. This increased perceptual complexity likely contributed to the emergence of significant novelty preference only at the third trial pair, suggesting that infants required repeated exposure to the novel triplets to update and refine their memory representation of the familiar rule and effectively discriminate it from the novel rule. The current findings extend previous demonstrations of visual RL for non-adjacent repetition-based patterns (ABA) in infants at least from 7 months (e.g.,[9]). However, the occipital brain localization of the association between neural entrainment and novelty preference may suggest that infants' performance primarily reflects a bottom-up detection mechanism relying on positional repetition cues rather than genuine rule abstraction. To disambiguate this question, future research should replicate the current study by directly comparing infants' performance on two repetition-based patterns, both involving adjacent repetitions (e.g., late repetition: ABB versus early repetition: AAB).

This study offers novel insights into the neural mechanisms underlying visual Rule Learning (vRL) in preverbal infants. Using EEG frequency-tagging, we demonstrate for the first time that the infants' brain rapidly attunes to repetition-based structures within continuous streams of visual stimuli. While previous research has extensively documented infants' vRL abilities using post-exposure behavioral tasks (e.g.,[9,10], this study provides a window into the neural processes underlying this capacity during real-time stimulus exposure. Our findings suggest that the infant brain efficiently detects visual structures, relying heavily on bottom-up processing and exogenous attention as a result of limited higher-order cognitive resources[1,39]. This infants' learning characteristic differs from that found in adults, whose cognitive systems exhibit a distinct learning trajectory, potentially relying more on top-down processing and displaying reduced sensitivity to predictable cues in the stimuli. The observed heightened sensitivity to structures in infancy is likely adaptive, supporting the construction of robust mental representations of the surrounding world, as exemplified in language acquisition[37] and action understanding[47]. These findings underscore the crucial role of early-life neural sensitivity to environmental patterns in shaping cognitive development and highlight the dynamic nature of learning across the lifespan.

Methods

All infants' parents and all adult participants provided written informed consent prior to the start of the experiment. The study protocol adhered to the ethical standards outlined in the Declaration of Helsinki (BMJ 1991; 302:1194), and received approval from the ethics committee of the University of Milano-Bicocca.

Participants

The final adult sample comprised 30 young adults (24 females, *M*age = 21.78 years; *SD* = 1.83; range = 19–27 years). All of them were either undergraduate or graduate university students receiving course credits for their participation or were recruited from the community through word of mouth. Eight additional adults were excluded from the final analyses due to technical problems (*N* = 3), excessive EEG artifacts (*N* = 1) or lack of entrainment to the base frequency (*N* = 4; see the Method section for further details). All participants self-reported Italian as their native language. The final infant sample comprised 27 9-month-old healthy infants (14 females, *M*age = 290 days; *SD* = 7; range = 276–302 days). All were born full-term with normal birth weight (*M* = 3,279 g, *SD* = 0.477 g), and met the screening criteria for normal delivery (gestational age > 37 weeks). None of the infants had any history of neurological, visual, or auditory impairments, and all parents reported Italian as their native language. Twenty-three additional infants were tested but excluded from the study due to fussiness (*N* = 7), excessive artifacts in EEG recordings (*N* = 7), or a lack of entrainment to the base frequency (*N* = 9; see the Method section for further details). The infant sample size is comparable to previous electrophysiological studies investigating transitional probabilities in auditory streams (e.g.,[23]).

Materials

The testing session was conducted in a quiet and well-lit room with an audiometrically and electrically shielded cabin. Participants were seated on their parents' lap approximately 60 cm from a 24-inch computer monitor. Parents were instructed to remain as still as possible and refrain from communicating or interacting with their infants throughout the session. Stimulus presentation was controlled by a custom MATLAB (v2014b; Mathworks Inc.) script (adapted from[48]). The stimuli consisted of 24 unique colored shapes. Each shape was embedded within a virtual square that varied in size from approximately 13.6 × 13.6° to approximately 16.6 × 16.6° of visual angle. All shapes were equalized in luminance. The experimental session was recorded by an infrared video camera discreetly positioned above the monitor and connected to the data acquisition computer. Stimuli consisted of 24 unique colored and shaped images presented against a light gray background; 16 images were shown during the learning phase and 8 were shown during the test phase. The task consisted of two phases: a learning phase and a test phase (Fig. 5). During the learning phase, stimuli were presented on the screen periodically at a fixed rate of six cycles per second (6 Hz; base stimulation frequency), without breaks or fixation periods. Participants were exposed to a continuous flow of visual triplets organized into ABA rules (e.g., square-arrow-square, circle-hexagon-circle) with each shape presented for 167 ms. Thus, the frequency of each ABA triplet was 2 Hz (6 shapes per second / 3 shapes per triplet, corresponding to 2 triplets per second). EEG amplitude at this frequency and its harmonics (multiple integers, $2 \times 6/3 = 4$ Hz, $3 \times 6/3 = 6$ Hz, $4 \times 6/3 = 8$ Hz, etc.) served as an index of the visual system's discrimination of the ABA rule. The learning phase consisted of 240 repetitions of the triplet, resulting in a total duration of 2 min. Each shape was drawn randomly from the pool of 16 and presented in a randomized order within the ABA rule, ensuring that no shape was presented consecutively across different triplets. To maintain participants' attention to the screen, a brief sound was delivered at random intervals, averaging 10 ± 3 s. Sequences were initiated manually by the experimenter when participants were attentively fixating the screen. During the learning phase, infants' looking behavior was coded from the recorded videos. On average, infants looked at the sequences for 87.34 s (*SD* = 21.98 s; minimum = 66.48 s; maximum = 112.56 s), corresponding to approximately 76% of the total presentation time. This confirms that the infants consistently attended to the visual stimuli throughout the exposure period. Following the learning phase, during which the EEG signal was continuously registered, participants were behaviorally tested on their ability to discriminate and generalize the learnt rule. Both infants and adults underwent the test phase. Infant performance was assessed by measuring looking times, while adult performance was assessed by measuring response accuracy. To evaluate participants' ability to generalize the familiar rule to new items, test triplets were composed of novel images differing in form and color from those used during habituation. Eight novel shapes—two assigned to the A group and two to the B group—were randomly combined to create four ABA triplets (familiar rule) and four ABB triplets (novel rule). Within each triplet, shapes were centrally displayed on the screen for 330 ms (after 9). Following the disappearance of the third shape, a 500-ms blank screen was presented before the onset of the next triplet. Infants were exposed to six test trials alternating between ABA and ABB triples while their looking behavior was recorded. The order of test trial order (i.e., novel first or familiar first) was counterbalanced across participants. Adults were presented with the same six test trials alternating between ABA and ABB triplets, with trial order counterbalanced across participants. They were instructed to verbally indicate as quickly and accurately as possible whether each presented sequence was familiar or novel compared to the one shown during the learning phase. Specifically, the instruction was: "Now you will see sequences of images different from the previous ones in shape and color. The images may follow the same pattern as in the previous phase or a new pattern. Please indicate whether the pattern is the same as in the previous phase or not".

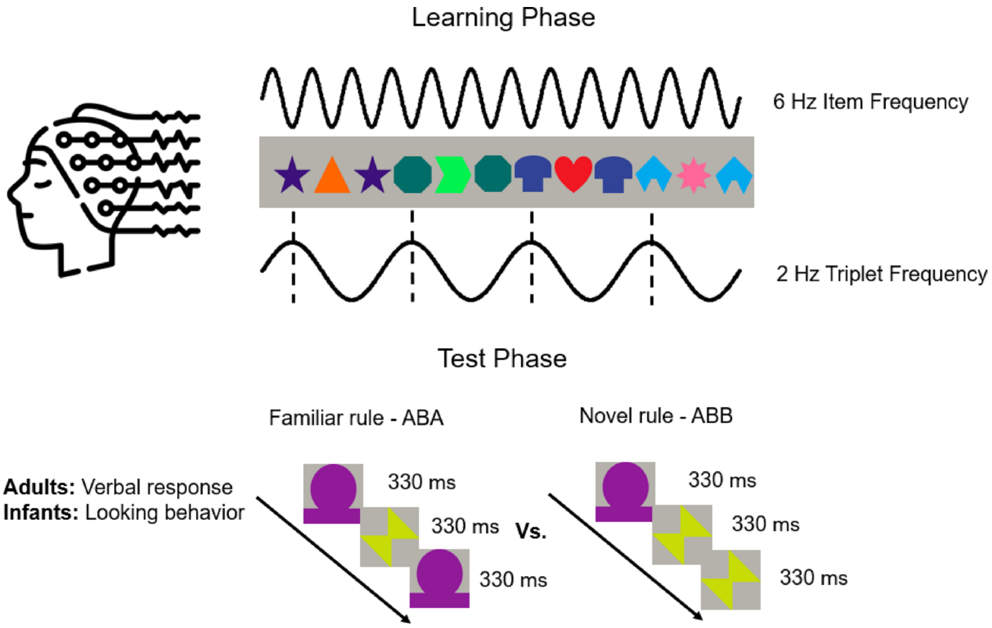


Fig. 5. During the learning phase (2 min), shapes were presented continuously at the center of the screen for 166.67 ms (6 Hz) while EEG was recorded. In the test phase, six trials alternated between familiar and novel rules, with stimuli presented for 330 ms each at the center of the screen. Adults provided verbal responses, while looking behavior was recorded for infants.

EEG recording and processing

EEG data were recorded through a 128-electrode HydroGel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, Oregon, United States), with the vertex electrode (Cz) serving as the reference. Signals were digitized by an EGI NetAmps 300 at a sampling rate of 500 Hz and filtered online with a band-pass filter of 0.1–100 Hz. Electrode impedances were checked online before the session started, and only those below 50 KΩ were considered acceptable. We applied a series of processing steps using Letswave 6 (https://nocions.webnode.com/letswave) and MATLAB 2012b (The Mathworks, Natick, MA, USA). Our processing pipeline mirrored established procedures outlined in several recent studies (e.g.,[49]). The first step involved the removal of peripheral electrodes located in the outermost ring near the base of the skull. Specifically, channels 43, 48, 49, 56, 63, 68, 73, 81, 88, 94, 99, 107, 113, 119 and 120 were excluded due to their high susceptibility to noise, which results from poor connectivity and frequent signal contamination, particularly in infant recordings (see[50]). Subsequently, we applied a fourth-order Butterworth band-pass filter with a frequency range of 0.1–100 Hz and a slope of 24 dB/octave to further eliminate unwanted frequencies. The signal was then segmented into 60 s epochs (16,000-time bins in total). Next, channels with exceptionally high amplitudes (exceeding 0.1 µV) were identified through visual inspection by an experienced observer. Manual detection for channel rejection has been previously validated in similar visual statistical learning and frequency tagging studies and frequency tagging analysis have been previously validated in similar visual statistical learning studies (e.g.,[23,51]). These channels were replaced with the average voltage calculated from up to six neighboring channels (*M*channes interpolated in the adult sample = 3.43, *SD* = 2.92; *M*channels interpolated in the infant's sample = 10, *SD* = 5.79). Following this correction, a common average reference was computed for all channels to minimize background noise. The preprocessed data were then segmented into epochs of varying lengths to suit different analysis objectives. Epochs of 120 s were used to evaluate responses across the entire exposure period. To capture the finer details of the learning process and its temporal dynamics, we employed 10 s epochs (each corresponding to 20 triplets), for a total of 12 epochs. Lastly, 60 s epochs, were utilized to compare signal amplitudes at the beginning (0–60 s) and end (61–120 s) of the learning phase, aiming to assess their relation with the ability to distinguish between novel and familiar test sequences. Frequency domain analysis was conducted on the EEG filtered data. A FFT was applied to each segment to extract amplitude spectra for all channels (calculated as the square root of the sum of squares of the real and imaginary parts divided by the number of data points). A common average reference computation was applied to all channels, followed by a discrete Fourier transformation (dFT) implemented via a FFT algorithm. A Hanning window was applied to the data, providing only the first half of the spectrum and normalizing the amplitude. The frequency resolution varied based on the epoch length: 0.008 Hz for the 12 s epochs (1/120 = 0.008), 0.1 Hz for the 10 s epochs (1/10 = 0.01), and 0.016 Hz for the 60 s epochs (1/60 = 0.016). To quantify activity within predefined frequency bins, two different baseline-corrected amplitude measures were calculated. For the 120- and 60 s epochs, BCA was achieved by subtracting the average amplitude of 12 surrounding frequency bins (6 on each side, excluding the immediately adjacent bins) from the amplitude at the frequency of interest. For the 10 s epochs, the correction used 6 surrounding bins (3 on each side) due to the reduced frequency resolution. Signal-to-noise ratio (SNR) values were computed for the 120- and 60 s epochs by dividing the amplitude at the frequency of interest by the average of 12 neighboring frequency bins. For the

10 s epochs, SNR was calculated using the 6 neighboring frequency bins. We then calculated the Z-score for each frequency bin by computing the difference between the amplitude at the frequency of interest and the mean amplitude of 12 surrounding bins, divided by the standard deviation of those 12 bins. Based on previous infant FPVS studies (e.g.,[52], recommendations in 51), only participants with a Z score of at least 2 at the base frequency (6 Hz) and/or its harmonic (12 Hz) in the 120 s epochs for occipital electrodes (specifically, electrodes 70, 75, and 83) were included in the subsequent analyses. Four adults and 9 infants were excluded from the analyses based on this criterion. Following the initial data processing, significant harmonics were identified and summed separately for the base frequency (6 Hz) and the rule frequency (2 Hz). Two ROIs of interest were selected based on prior research and visual inspection of the data. The frontal ROI included channels 3, 4, 5, 10, 12, 18, 19, 20, 23, 24, 118, and 124, the occipital comprised channels 65, 66, 69, 70, 71, 74, 75, 76, 82, 83, 84, 89, and 90. The selection of significant harmonics for analysis of base and rule frequencies was based on Z-scores, calculated separately for each ROI and group. A Bonferroni-corrected significance threshold was applied, set at a Z-score of 2.66 for the occipital ROI (0.05/13 channels = 2.66) and 2.75 for the frontal ROI (0.05/12 channels = 2.75). In the occipital ROI, infants showed significant responses at the rule frequency from the 1st (2 Hz) to the 8th (16 Hz) harmonic (excluding the 3rd, 6th, 9th, and 12th harmonics, which correspond to the base frequency). In contrast, adults exhibited significant responses from the 2nd (4 Hz) to the 11th (22 Hz) harmonic. Given that the stimulation frequency was 2 Hz, this frequency was incorporated in the summed response for this group, despite control analyses on BCA amplitudes confirming that the significance of the response patterns was unaffected by the inclusion or exclusion of the 2 Hz response (see SI Results). For the baseline response, infants' significant harmonics extended up to the 4th harmonic (24 Hz), while adults' significant harmonics extended up to the 5th harmonic (30 Hz). For the segmented signals (10 s and 60 s epochs), we applied the same harmonics as for the 120 s epochs. To determine the presence of significant responses at the base and rule frequencies within each ROI, after summing across the significant harmonics, Z-scores were calculated for the averaged individual amplitude spectra across the respective electrodes.

Statistical analysis

To identify group differences in neural activity, we conducted LMM analyses using the lme4 package[53] in R (version 4.2.3; 2022). Default Satterthwaite approximations for degrees of freedom were employed, which are well-suited for datasets with smaller sample sizes and fewer data points per subject[54]. For the analysis, occipital channels were grouped into three ROIs: left (channels 65, 66, 69, 70), medial (channels 71, 74, 75, 76, 82), and right (channels 83, 84, 89, 90). Similarly, frontal channels were grouped into two neuroanatomically defined ROIs: left hemisphere (channels 3, 4, 5, 10, 12, 18) and right hemisphere (channels 19, 20, 23, 24, 118, 124). The mean amplitude of the BCA signal, which includes the highest consecutively significant harmonics for each response (base and rule) and cortical ROIs (occipital and frontal), was extracted for each participant during the 120 s learning phase. For the occipital ROI, a LMM was fitted with BCA as the dependent variable, Group (adult, infant) and ROI (left, middle, right) as fixed categorical predictors, and Participant as a random intercept to account for within-subject variability. A similar LMM was applied to the frontal cortex, with the same fixed effects (Group: adult, infant; ROI: left, right) and random intercept structure.

To investigate learning curves across the 120 s exposure period, we ran separate LMMs on BCA amplitude for each cortical ROI, analyzing the twelve 10 s epochs. Models including ROI and segment as fixed factor were fitted for adults and infants separately, following the approach outlined in Kersey and Emberson[55]. Each model included a linear and a quadratic term to examine both linear and non-linear trends in the data. To account for individual differences and within-subject variability across epochs, we included a random intercept for each participant and random slopes for both the linear and quadratic terms of the epoch variable (e.g., 1 + poly (10 s epoch) | Participant). This allowed us to consider changes across epochs as within-participants comparisons, rather than treating each epoch as an independent observation. Separate models were then conducted for both the rule frequency (2 Hz, learning trajectory) and the base frequency (6 Hz, general visual response), allowing us to examine learning-specific changes in entrainment to the rule structure, as well as changes in general visual response to the visual images (6 Hz) across the exposure period.

To investigate the behavioral outcome of learning, specifically whether participants could discriminate between familiar and novel rules and generalize the familiar rule to novel items during the test phase, we conducted two separate analyses for each group. For adults, a one-sample *t*-test was conducted to compare the proportional accuracy of correctly detecting the familiar and the novel rule (number of correct responses/total number of responses) to chance performance. For the infants' group, we used an LMM with logarithmically transformed looking times as the dependent variable. The model included Test Trial Pair (first, second, third), Test Trial Type (familiar and novel), and Test Trial Order (familiar-novel, novel-familiar) as categorical predictor variables, and Participant as a covariate and random intercept.

Finally, to investigate the relationship between brain activity at the rule frequency and participants' behavioral performance during the test phase, we conducted a series of fixed-entry multiple regression analyses separately for each cortical ROI and age group. Rule frequency BCA amplitude during the first and second 60 s epochs of the learning period was included as predictor variable. This approach allowed us to examine how variations in neural activation during distinct stages of learning influenced behavioral outcomes. For the infant group, the dependent variable was the novelty discrimination score, calculated as the log-ratio of looking times to novel versus familiar test trials (log (looking time to novel – familiar)/log (looking time to novel + familiar). For the adult group, the dependent variable was the proportional accuracy during the test phase.

Data availability

All data have been made publicly available via the Open Science Framework (OSF) and can be accessed at https://osf.io/uy59c/?view_only=830b2f667a37421aa35ad8f74c43c467.

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Author contributions

R.B., H.B., and V.M.C. designed research. R.B. and V.S. performed research. R.B., V.S., and S.P. analyzed data. R.B. wrote the main manuscript text, and S.V. wrote the method section. All authors reviewed the manuscript.

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Declarations

Competing interests

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Additional information

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